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Abstract

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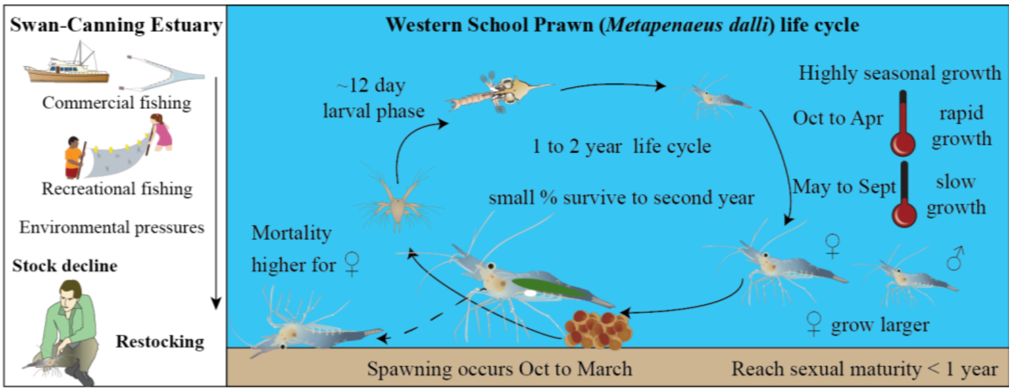
Graphical Abstract (for review)

Highlights

- *Metapenaeus dalli*, an iconic recreational species, is being evaluated for restocking.
- Highly seasonal growth, with most occurring in summer and little to none in winter.
- Females grow significantly larger than males and have greater mortality rates.
- Gravid females are found only when water temperatures are greater than 20 °C.
- Prawns larger and current population biomass is lower than 30 years ago.
- Prawns should be released in summer to maximise growth and increase survival.

Graphical abstract



Estimating biological parameters for penaeid restocking in a temperate Australian estuary

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Abstract

Robust estimates of growth, mortality and reproduction provide fundamental information for evaluating release programs. Length frequency data and mixture analysis were used to estimate a suite of biological parameters for the Western School Prawn (*Metapenaeus dalli*). This was an iconic recreational species, which is being evaluated for restocking in the Swan-Canning Estuary in temperate, south-western Australia. Monthly length frequency data, collected from hand and otter trawls over 26 consecutive lunar cycles showed that *M. dalli* exhibits highly seasonal patterns of growth and reproduction. Growth occurred predominantly during the warmer months (October-March), with little to no growth in cooler months (May-August). A von Bertalanffy growth model, incorporating seasonal growth, estimated that female prawns grew significantly larger (L_∞ = 33.6 mm CL) than males (L_∞ = 22.8 mm CL), but that the rate of reaching the asymptotic size was the same for both sexes (K = 0.98). Gravid females were found only from October to March and spawning activity was greatest from November to February, when surface and bottom water temperatures ranged from 20 to 28 °C. The instantaneous rate of total mortality (Z) was greater for females (0.069 week^{-1} $\cong$ 3.57 year^{-1}) than males (0.043 week^{-1} $\cong$ 2.28 year^{-1}). Since fishing mortality is now very low, these estimates provide a close approximation to natural mortality (M). A similar approach was applied to estimate the growth parameters from the length distributions of *M. dalli* reported in this system 30 years earlier, when the population biomass was likely to be much higher than the current biomass and *M. dalli* was heavily exploited by recreational fishers. The maximum size and L_∞ of *M. dalli* are now between 10 and 20% larger than 30 years previously, which may reflect the current lower fishing pressure and lower population biomass. From this study, the optimal release times for *M. dalli* are from December to March, when prawns grow rapidly and can be cultured successfully under current production systems.

Keywords: stock enhancement; prawn/shrimp; growth; mortality; *Metapenaeus dalli*; Swan-Canning Estuary

1. Introduction

Individuals from a several species of prawns or shrimp in the Penaeidae are released on a very large, commercial scale (hundreds of millions to billions) in Japan (Hamasaki and Kitada, 2006) and China (Bell et al., 2005; Wang et al., 2006; Loneragan et al., 2013). Smaller scale, commercial releases of penaeids have also been practised in Kuwait, Sri Lanka, the United States and Australia (Bell et al., 2005; Loneragan et al., 2013). Recent research in Australia has focussed on release programs for penaeids to “enhance” recreational fishing; one for Eastern King Prawns *Penaeus plebejus*, to overcome recruitment limitation caused by a physical barrier to prawn larval recruitment (Taylor, in press) and the second, to investigate the potential for rebuilding the stocks of the Western School Prawn *Metapenaeus dalli* (this study), i.e. evaluating the potential to restock this species.

The genus *Metapenaeus* comprises nearly 30 species that are found exclusively throughout the inshore coastal and estuarine waters of the Indo-West Pacific (De Grave, 2010) where they contribute to important commercial and recreational fisheries (Dichmont et al., 2006; Kompas et al., 2010). For example, in subtropical and temperate New South Wales, Australia, an average of 1,410 tonnes of prawns, valued at more than AUD $18 million, were caught annually between 2004 to 2009, in nearshore and estuarine environments, with *Metapenaeus macleayi* and *M. bennettae* comprising 54% and 32% of the total catch by weight and value, respectively (Montgomery, 2010). Prawns found in the estuaries of this region, predominantly *P. plebejus* and *M. macleayi*, are also exploited by recreational fishers who catch ~4,700 tonnes annually (Montgomery, 2010).

Metapenaeus dalli is the only metapenaeid found in temperate south-western Australia (Racek, 1957). This species typically occurs in shallow, inshore marine waters (< 30 m deep) along the western coast of Australia from Darwin in the north to Cape Naturaliste in the south and also in Java, Indonesia (Grey et al., 1983). However, in latitudes south of 31º S, it is found only in estuaries and is believed to complete its entire life cycle within these systems (Potter et al., 1986; 1989), with larval development lasting ~12 days (Crisp et al., 2016).

Metapenaeus dalli is thus classified as a solely estuarine species in this region (Potter et al., 2015).

Both *M. dalli* and the Western King Prawn *Penaeus latisulcatus* were the focus of a small commercial and iconic recreational fishery in the Swan-Canning Estuary. The commercial fishery catch peaked at 15 tonnes in 1959, but then declined, leading to its closure in the mid-1970s (Smith, 2006). At its peak, recreational prawning in this estuary involved over 50,000 people and became an iconic pastime, particularly during the Christmas period (Smithwick et al., 2011). However, recreational catch rates also declined, with the last significant catches recorded in the late 1990s. The reasons for the decline are unclear but are likely due to a combination of overfishing, changing environmental conditions and recruitment failure (Smith, 2006; Smith et al., 2007). Smith et al. (2007) concluded that despite the large reduction in fishing pressure, *M. dalli* populations were still low and had not recovered. They attributed this lack of recovery to the small, discrete breeding stock that was not at large enough to rebuild the population through self-replenishment. Thus, given the long-term recruitment failure, restocking was seen as a possible means of increasing the population size of *M. dalli* in the Swan-Canning Estuary by bypassing the recruitment bottleneck during the high mortality stages from larval to young juvenile prawns.

In response to the depleted status of the *M. dalli* population in the Swan-Canning Estuary, a trial restocking program was initiated. This study is part of the associated research program and focuses on estimating the biological parameters of the school prawns to provide the information to better evaluate the costs and benefits of restocking and optimise the potential success of releases. The overall objective of this study is to use the data from the systematic, intensive sampling program of *M. dalli* in the Swan-Canning Estuary in 2013/14 and 2014/15 to determine, for the first time, the biological parameters for growth, mortality and size at maturity to evaluate optimal release times. Growth curves were also fitted to the historical data collected over 30 years ago (1977 to 1982, Potter et al., 1986) when the biomass of the population, catch and intensity of recreational fishing effort were much higher than currently.

2. Material and methods

2.1. Study area

The Swan-Canning Estuary (Fig. 1) in south-western Australia, is ~50 km long and covers an area of ~55 km^2 (Valesini et al., 2014). This drowned river valley system is permanently-open to the Indian Ocean via a narrow entrance channel that opens into two basins and the tidal portions of the Swan and Canning Rivers. Although the majority of the estuary is shallow, *i.e.* < 2 m in depth, it reaches a maximum depth of ~20 m in the entrance channel. The region experiences a Mediterranean climate, with hot, dry summers and cool, wet winters (Gentilli, 1971). Approximately 70% of the rainfall occurs between May and September (Hodgkin and Hesp, 1998), leading to marked seasonal variations in environmental conditions in the estuary: salinities are stable and relatively high throughout much of the estuary during the austral summer (December to February), but during winter, may vary markedly along the estuary following substantial freshwater discharge (Tweedley et al., 2016a).

The estuary flows through the capital city of Perth, which supports ~78% of the 2.6 million people in the state of Western Australia (Australian Bureau of Statistics, 2015). Both the estuary and its catchment have been highly modified by anthropogenic activities (Commonwealth of Australia, 2002), which has led to multiple stressors on the system, such as the increased delivery of sediments and nutrients, in addition to changes to salinity and hydrological regime, including periodic hypoxia (Stephens and Imberger, 1996; Tweedley et al., 2016b). Despite these perturbations, the estuary is valued highly by the Western Australian community for its aesthetic, commercial, environmental and cultural importance and recreational fisheries (Malseed and Sumner, 2001).

2.2. Rainfall and physic-chemical data for the Swan-Canning Estuary

Rainfall data for Perth airport were obtained from the Bureau of Meteorology (http://www.bom.gov.au/climate/data/) from October 2013 until October 2015. Weekly data for salinity and temperature throughout the water column were obtained for sites in the Swan-Canning Estuary from the Department of Water (http://wir.water.wa.gov.au) for the same period.

2.3. Sampling procedure

Prawns were sampled at night at 20 nearshore (< 2 m deep) sites using a hand trawl net and 16 offshore sites (2-17 m deep) using a small otter trawl net, on each new moon phase (i.e. every 28 days when the moon < 10% illumination) between October 2013 and October 2015 (i.e. 26 lunar cycles over two years) . Note that, due to a mechanical failure, no samples were collected from the offshore sites in December 2014 and thus the corresponding data from the nearshore waters was also excluded for this lunar cycle. The sites extended from close to the mouth of the Swan-Canning Estuary to ~34 and ~27 km upstream in the Swan and Canning rivers, respectively (Fig. 1). The total area within the bounds of the sampling sites was 35 km^2, with 15.5 km^2 in nearshore water and 19.6 km^2 in offshore water.

Nearshore sites were sampled using a 4 m wide hand trawl constructed from 9 mm mesh. The width of the hand trawl net during trawling was, on average, ~2.85 m, but varied slightly amongst trawls depending on the condition of the substratum, presence of submerged obstacles and localised wind and wave conditions. Two replicate trawls of 200 m (swept area of ~570 m^2, were carried out at each site on each sampling period and on any single lunar cycle covered a total area of 22,800 m^2. A 2.6 m wide otter trawl net, with 25 mm mesh in the body, and 9 mm mesh in the cod end was employed to sample prawns in the offshore waters. The net was towed at a speed of ~1.6 knots (~3 km h^{-1}) for 5 min, covering a distance of ~250 m. Two replicate trawls of ~650 m^2 were completed at each site on each sampling period covering a total area of 20,800 m^2 at the 16 sites. After each trawl, individuals of *M. dalli* were euthanised in an ice slurry and returned to the laboratory to be sexed, measured and weighed, expect when > 50 prawns were caught. In such instances, a small sub-sample (~50 individuals was retained) and the majority of prawns were identified, sexed and measured (see below) in the field and returned alive to the water.

The catchabilities of the hand trawl and otter trawl nets used in this study have not been estimated. A catchability of 0.4 has been used in the estimation of the biomass of *M. dalli* in the estuary, based on a range of estimates for catching juvenile *Penaeus esculentus* and *P. semisulcatus* in a small beam trawl (Loneragan et al., 1995) and those for *P. latisulcatus* in a large, commercial otter trawl (Joll and Penn, 1990)

In the laboratory, the carapace length (CL), i.e. orbital indent to the posterior edge of the carapace, of each individual was measured (0.01 mm) using digital vernier callipers, and the wet weight (0.01 g) and sex of the prawn were also recorded. Females were identified by presence of a thelycum and males by the presence of a petasma. Individuals without a thelycum or petasma were recorded as juveniles. Female prawns were also inspected to determine if they were gravid, i.e. had large green ovaries, as described by Tuma (1967) and Crisp et al. (in press) and/or possessed a spermatophore.

2.4. Length-weight relationship

Initially, the relationship between carapace length (CL) and wet weight (W), was evaluated with a non-linear least squares (NLS) model in *R* (R Core Team, 2014). Since the residuals increased with increasing CL, a log relationship ($log(W) = log(a) + blog(CL)$) was calculated. A bias correction factor for back-transforming mean weight values for a given length was calculated using:

$$e\frac{s^2{}_{Y|X}}{2},$$

where $s^2{}_{Y|X}$ is the mean square error from the linear model (Ogle, 2014).

The length-weight relationships for female and male *M. dalli* were:

$$\text{Female: } \log(W) = -6.29 + 2.68\log(CL)\text{, } (R^2=0.98, n=1{,}721);$$

$$\text{Male: } \log(W) = -6.78 + 2.89\log(CL)\text{, } (R^2=0.98, n=1{,}394).$$

Alternatively, on the original scale, with bias correction:

$$\text{Female: } W = (0.0019CL^{2.68}) \times 1.0067;$$

$$\text{Male: } W = (0.0011CL^{2.89}) \times 1.0058.$$

2.5. Estimating growth

The length frequency data from hand and otter trawls were used to estimate growth and mortality. Growth was estimated from the pooled data from both the hand and otter trawls after adjusting for swept area (see below) by mixture analysis and modal progression. Growth estimates for *M. dalli* in 1977-82 were calculated from modal progression using the data in Potter et al. (1986).

In the absence of data on net efficiency, the catchability of *M. dalli* using the hand and otter trawls were assumed to be equal, and the length frequency data from the otter trawls were scaled up by a factor of 1.096, i.e. the ratio of the total swept area of hand trawls: otter trawls each sampling period (i.e. 22,800 m^2: 20,800 m^2). Juveniles were assigned equally to each of the female and male groups. The CL measurements from these data were then allocated to 1 mm size classes.

Identifying cohorts

Monthly histograms of the weighted 1 mm CL data were created in *R* and reviewed visually to gain an understanding of changes in length frequency distribution over time and identify potential modal groups (cohorts). Finite mixture analysis was conducted in *R* using the Mixtools package (Benaglia et al., 2009). Starting values for the mean, standard deviation

(SD) and weighting for each potential mixture component (cohort) in a monthly sample were estimated from the histograms visually. A two-step iterative process was employed to generate normal distributions for each of the components using the Expectation-Maximisation (EM) algorithm from the Mixtools package (Benaglia et al., 2009). Hypothesis testing ($a = 0.05$) using 1,000 bootstrap replicates was used to produce a likelihood ratio statistic for the null hypothesis of a k component fit versus an alternative hypothesis of $k+1$ (up to a maximum of 10) components for each monthly sample (Benaglia et al., 2009). The resultant outputs were optimised estimates of the mean, SD, weighting and number of prawns in each mixture component for each monthly sample.

Analysis of historical data

Data on the biology of *M. dalli* in the Swan-Canning Estuary collected by Potter et al. (1986) between 1977 and 1982 were analysed to estimate growth rates for comparison with the current study (2013/15). These authors used the same sized mesh in the otter trawl (25 mm), but employed a larger mesh (19 mm) in the hand trawl compared to that used in the current study (9 mm). The means and SD of the female and male CL frequency distributions were estimated visually from Fig. 3 in Potter et al. (1986). These data were used to reproduce the Potter et al. (1986) modal progression graph in *R*.

Parameter estimation from length frequencies

The methods outlined in this section were applied only to the 2013/15 data, because the original length frequency data were not available from the historical study. The primary purpose of estimating parameters from length frequencies was to create a set of robust starting values for the growth models.

The weighted 1 mm size class length frequency data from the current study were grouped by sampling period and analysed using the Length Frequency Data Analysis 5 (LFDA 5; Kirkwood et al., 2001) and Fisheries Stock Assessment Tools II (FiSAT II) packages (Gayanilo et al., 2005a). In LFDA 5, the Hoenig and Hanumara (1982) and Pauly et al.

(1992) seasonal version of the von Bertalanffy growth function (VBGF) were fitted to the length frequency data using the ELEFAN (Pauly, 1987) method. A score grid search in LFDA 5 provided the initial parameter estimates, which were then optimised and plotted using the automatic maximisation process. Similarly, in FiSAT II, the ELEFAN I routine was used to directly fit a seasonal VBGF (Pauly et al., 1992), by using a response surface analysis and then plotting and optimising the fit by eye.

Parameter estimation from modal progression

The same method for estimating growth parameters by fitting a non-linear least squares (NLS) model to data derived from modal progression was used for the data from 1977-82 and 2013/15. For the earlier data, the modal progression graph recreated in *R* was used to model and estimate growth parameters. For the 2013/15 data, the means and SD from the finite mixture analyses were plotted separately for female and male prawns in a 26 lunar cycle time series. Modal progression was used to identify cohorts by tracking each point through time and visually observing its position relative to adjacent cohorts.

The Somers (1988) seasonally oscillating adaption of the VBGF was applied to estimate growth parameters for the cohorts of male and female prawns that could be followed in the carapace length frequency histograms for the longest period. The Somers adaptation is:

$$L(t) = L_\infty\left\{1 - e^{-[K(t-t_0) + S(t) - S(t_0)]}\right\}, \quad S(t) = (CK/2\pi)\sin 2\pi(t - t_s), \text{ and } S(t_0) = (CK/2\pi)\sin 2\pi(t_0 - t_s),$$

where $L(t)$ is the average length at time t, L_∞ is the asymptotic length, K is the rate at which the model reaches asymptotic length, t_0 is the theoretical time where the average length is 0. The functions $S(t)$ and $S(t_0)$ generate the seasonal oscillation of the growth curve: C controls the amplitude of the growth oscillation during the winter period (if $C = 1$ growth stops or if $C = 0$, growth is continuous, i.e. there is no seasonal oscillation), t_s is the start of the curved portion of the first growth oscillation.

The Somers (1988) model was fitted in *R* using the FSA (Ogle, 2014) and Minpack (Elzhov et al., 2013) packages. The former package provided an implementation of the Somers (1988) growth function and the Minpack package was used to implement an NLS function using a modified Levenberg-Marquardt algorithm, which supports lower and upper parameter constraints. The starting values for the NLS model (L_∞, K, t_0, C and t_s) for the 2013/15 and historical data (1977-82) were estimated by averaging the results of L_∞, K, t_0, C and t_s from the length frequency analysis using LFDA 5 and FiSAT II. The following parameters were constrained to optimise model fitting: C between 0 and 1, t_0 between -1 and 0 and t_s between -1 and 1.

The NLS model assumes that the data are homoscedastic and the errors are normally distributed. These assumptions were investigated by (1) plotting the residuals and fitted values for each model and visually verifying the distribution of the plotted points and (2) creating histograms of the residuals and visually checking the distribution for symmetry around the midpoint. A bootstrapping technique using 1,000 resampled data sets was used to create 95% confidence intervals (CI) for each of the estimated parameters.

2.6 Estimating total mortality

Instantaneous total mortality (Z) was estimated separately for female and male prawns using the weighted 1 mm size class length frequency data from the 2013/15 data set. A catch curve regression was implemented in *R* using length-converted catch curves (LCC; Pauly, 1983a,b; 1984). Both seasonal length-converted catch curves (SLCC; Pauly, 1990) and non-seasonal LCC were fitted to the data. Only the results from the LCC are presented below. The non-seasonal LCC method was implemented with:

$$\log\left(\frac{N_i}{\Delta t_i}\right) = a + b \times t_i, \text{ and}$$

$$t_i = t_0 - \left(\frac{1}{K}\right) \times \log\left(1 - \frac{i}{L_\infty}\right),$$

where N is the number of *M. dalli* in length class i, Δt is the time it takes prawns to grow through length class i, t is the relative age at the mid-length of class i (calculated using the inverse von Bertalanffy growth equation), and the absolute value of b becomes an estimate of Z. The non-seasonal LCC was chosen to estimate Z as a recent study by Hufnagl et al. (2013), evaluating eight methods for estimating Z, found that the non-seasonal LCC method was consistently rated among the most accurate of methods for both seasonal and non-seasonal growth scenarios. They also found that when mortality was low (i.e. < 5 year^{-1}), the non-seasonal LCC was in general, a suitable choice for estimating Z.

2.7. Time and size at maturity

Gravid female prawns, i.e. stages 3 and 4 of Tuma (1967) and Crisp et al. (in press), were readily identified macroscopically by the appearance of a distinct green gonad. The maturity schedule assumes that there is a difference between morphologically mature prawns, i.e. prawns that have grown to 21 mm CL, the size at which 100% of the population is capable of being mature (see results Fig. 5), and will cycle between ovigerous and non-ovigerous stages of maturation, and functionally mature prawns, i.e. ovigerous individuals, currently appearing gravid.

The relationship between size and the presence of gravid ovaries was examined for female prawns by using data containing all prawns for each sampling month when gravid prawns were present, i.e. October to March. A histogram of gravid prawns was constructed using 1 mm CL size classes to identify the smallest and largest length class containing mature prawns. Prawns between these length classes represent an approximate proportion of the female population shifting from an immature to a mature state. This transition was evaluated with logistic regression using a logit transformation in a general linear model (GLM) using *R* and the formula:

$$log\left(\frac{p}{1-p}\right) = a + b_1 X$$

where: p is the proportion mature and $1 - p$ is the proportion immature; a and b_1 are model parameters and X is the CL in mm. The CLs where 50% (CL_{50}) and 90% (CL_{90}) of the female prawn population were gravid were calculated using:

$$X = \frac{log\left(\frac{p}{1-p}\right) - a}{b_1}$$

where p is 0.5 (50% mature) or 0.9 (90% mature), a and b_1 are model parameters. Confidence intervals for CL_{50} and CL_{90} were created by bootstrapping 1,000 samples using the bootCase function from the Car package in *R* (Ogle, 2014).

3. Results

3.1. Rainfall and environmental data

The total rainfall for the 12 months from October 2013 to September 2014 was 599 mm, with most occurring between May and September and very little to none between December and February (Fig. 2). The rainfall from October 2014 to September 2015 followed the same pattern as that for 2013/14, but was slightly lower than in the previous 12 months (Fig. 2). Average maximum air temperatures varied seasonally with the lowest values (18 to 19 ºC) recorded in July in 2014 and 2015 and the highest (33 to 34 ºC) in January and February. The seasonal patterns of air temperature in 2014/15 followed those of 2013/14 very closely, except that November was 4 ºC warmer in 2014/15 (Fig. 2).

The seasonal patterns of change in water temperature were similar in the five regions of the Swan-Canning Estuary and in the two years of the study, with surface temperatures ranging from a minimum of 11.2 ºC in the Lower Canning Estuary (LC) during June 2014 to a maximum of 28.5 ºC in the Upper Canning Estuary (UC) in January 2014 (Fig. 3a). The lowest bottom temperatures were 14.4 and 15.1 ºC in August 2014 in the UC and Middle Swan Estuary (MS), respectively and highest in the UC in January 2015 (27.8 ºC; Fig. 3b).

The lowest range in surface water temperature (14.0 to 25.3 ºC) was recorded in Lower Melville Water (LM), and the highest range in the UC (12.7 to 28.5 ºC). Bottom temperatures varied less than those of the surface waters, with the greatest range in the UC (14.4 to 27.8 ºC).

Surface salinity ranged from 2.8 in the LC during October 2014 to 37.3 in that same region in March 2014 (Fig. 3c). With the exception of October 2013, salinities in LM waters were > 22, whereas in all other regions, they declined to ≤ 10. The lowest bottom salinity was 3.7 in the UC in October 2013, while the highest was 37.0 in the LC during April 2014 (Fig. 3d). The ranges in salinity varied markedly among the regions, from as little as 4.3 in LM (32.8-37.1) to 29.8 (3.7 to 33.5) in the UC.

3.2. Size structure of the population, time and size at maturity

A total of 10,570 *M. dalli* (5,631 females, 4,939 males) were caught during the 26 consecutive lunar cycles months between October 2013 and October 2015; 1,323 in the hand trawl net and 9,247 in the otter trawl (Fig. 4). The female prawns ranged from 6.5 to 30.5 mm CL and the males from 6.5 to 24.1 mm CL (Fig. 4). The smallest prawn, a 2.0 mm CL juvenile, was caught in hand trawls in January and February 2015 (Figs 6, 7). Two modes were evident in the length frequency distributions for otter trawl nets: one at 11 mm CL and a second, smaller mode at 17-18 mm CL (Fig. 4). The first mode was also present in the hand trawl nets although greatly reduced in magnitude, while the second mode in the hand trawl nets was slightly smaller (15-16 mm CL) than that in the otter trawls.

Gravid female *M. dalli* and those carrying a spermatophore were caught in the hand and otter trawls during November 2013 and March 2014 and between October 2014 and March 2015. These females ranged in size from 12.0 to 28.5 mm CL in 2013/14 and 10.0 to 30.0 mm CL in 2014/15. The greatest proportions of gravid females (39 and 54% in 2013/14 and 2014/15, respectively) and those carrying spermatophores (45 and 50% in 2013/14 and 2014/15, respectively) were recorded in January of both years. The estimated carapace length at 50%

maturity (CL_{50}) for females, based on the CL of gravid females, was 16.9 mm CL (95% Confidence Interval [CI] = 16.7 to 17.0 mm CL) (Fig. 5). The estimated CL_{90} for females was 18.5 mm CL (95% CI = 18.3 to 18.7 mm CL).

3.3. Growth

The smallest catches of females (n = 43) and males (n = 34) from otter trawls and hand trawl nets were recorded in October 2013 and the largest catch of females in November 2014 (447), while those of males were in December 2013 and April 2015 (326 and 323, respectively; Figs 6, 7). Three main cohorts (C, F and J, Fig. 6) represented about 77% of the total female *M. dalli* catch over the two year sampling period. One cohort (F) could be followed for 17 months from February/March 2014, when the mean size of young female prawns was 10 mm, until May 2015 when it had reached 26 mm CL (Figs 6, 8a). Three cohorts of male prawns (A, D and H, Fig. 7) accounted for nearly 90% of the total male *M. dalli* catch and one cohort (D) was followed for 19 months from February/March 2014 (mean size = 9.5 mm CL) until August 2015 (mean size = 19 mm CL) (Figs 7, 8b).

The growth curves derived from the mean carapace length distributions showed a highly seasonal pattern of growth in both years (Fig. 9a, b). This pattern was also observed when the seasonal growth model was fitted to the historical data collected between 1977 and 1982 (Fig. 9c, d). Fitting the growth data with non-linear least squares (NLS) growth models gave similar values of K for the current and historical curves for females (0.98 and 1.05, respectively) and males (0.98 and 1.01, respectively; Table 1). However, the estimated asymptotic mean carapace lengths (L_{∞}) for females (33.6 mm CL) and males (22.8 mm CL) in the 2013/15 data set were longer than those estimated for the historical values (females = 28.0 mm CL, males = 20.0 mm CL; Table 1). The value of the C parameter for both females and males was close to 1, indicating that growth almost stops for a period.

3.4. Mortality

The instantaneous total mortality (*Z*) for female *M. dalli* estimated from the non-seasonal length converted catch curve method (LCC) was 3.57 year^{-1}, about 56% higher than that estimated for males (*Z* =2.28 year^{-1}, Figure 10, Table 2). These values are equivalent to weekly rates of 0.069 week^{-1} for females and 0.043 week^{-1} for males (Table 2).

4. Discussion

This study used data collected during a recent comprehensive field study of the Western School Prawn *Metapenaeus dalli* in both nearshore (< 2 m deep) and offshore waters (2 to17 m deep) of the Swan-Canning Estuary to provide the first quantitative estimates of growth and mortality and female size at maturity. Growth and reproduction of *M. dalli* were highly seasonal, with faster growth and mature females recorded in the Austral late spring, summer and early autumn (October to March), when water temperature exceeded 20 °C and virtually no growth in late autumn and winter (May to August). This highly seasonal pattern of growth suggests that releases of aquaculture-raised small prawns in the late autumn and winter months are not likely to grow and as a consequence, may be very vulnerable to predation and much higher mortality than summer releases. Differences were also detected between the growth and mortality of males and females, with females growing to a larger size and experiencing a higher total mortality (*Z*) than males.

4.1. Reproduction

Metapenaeus dalli exhibits a strong seasonal cycle of reproduction in the Swan-Canning Estuary with gravid females, and females carrying a spermatophore, first appearing in October or November and last seen in March. During this period the average temperatures in the bottom waters of the five study regions varied from 20 to 28 ºC. A strong seasonal cycle of reproduction was also found in a less-intensive, but longer-term, study from 1977 to 1982 by Potter et al. (1986), who recorded gravid *M. dalli* between November and April. This pattern of reproduction defines the period that prawns can be cultured from wild inseminated females, unless the life-cycle is closed or prawns are held in captivity for extended periods of time and spawning is induced in the culture facilities. Thus, under current culture practices for *M. dalli* in Western Australia, where inseminated females are captured in the wild and used to produce eggs and larvae in culture, the time window for releasing cultured prawns is restricted mainly to the period from December to March. The over 30-year gap between sampling in the current study and Potter et al. (1986) indicates that the seasonal cycle established for *M. dalli* is unlikely related to a short-term events (e.g. a single weather event or response to an unusual estuarine condition). Thus, it is more than likely an evolutionary adaption of *M. dalli* to a seasonally oscillating reproductive cycle in response to longer-term hydrologic and climatic influences, in effect tuning itself with the estuarine environment (see Tweedley et al., 2016a). A similar conclusion was made by García (1988), while studying environmental effects on the population dynamics of *Penaeus notialis* in coastal waters of the Ivory Coast.

In addition to *M. dalli*, many fish species reproduce during the summer and early autumn in the estuaries of south-western Australian (i.e. estuarine species *sensu* Potter et al., 2015, Tweedley et al., 2016a), when freshwater discharge is limited (Hodgkin and Hesp, 1998). It has been suggested that in these microtidal estuaries, water movement via tidal exchange and freshwater discharge is restricted and thus environmental conditions remain fairly stable during summer and autumn and the eggs and larvae are not flushed out of the estuary (Tweedley et al., 2016a).

The initiation of reproductive activity in female *M. dalli* appears to be synchronised with an increase in surface and bottom water temperatures in the Swan-Canning Estuary to temperatures 20 ºC. The activity and emergence of benthic invertebrates is strongly influenced by temperature and the emergence time of several species of prawns increase greatly above this temperature (Hill, 1985; Wassenberg and Hill, 1994). Park and Loneragan

(1999) found that this pattern of activity was also demonstrated in two larger species of metapenaeids, *Metapenaeus endeavouri* and *M. ensis*. The months where reproductive activity was greatest (i.e. November-February) occur when the surface and bottom temperatures are between 20 and 28 ºC (Fig. 3a, b). This peak reproductive output (i.e. November to February) indicates a life history strategy by *M. dalli* to optimise larval survival between 20 and 28 ºC. Laboratory studies of the survival and growth of larval *M. dalli* under different temperature and salinity regimes found that survival and growth were greater at approximately 26 ºC than either 20 or 32 ºC (J. Crisp et al., Murdoch University, unpublished data). Preston (1985) also found that the survival and development of larval *Metapenaeus bennetae,* an species breeding in estuaries and marine waters on the east coast of Australia, were greatest in similar environmental conditions to those where the broodstock were collected..

The majority of *M. dalli* reaching reproductive maturity are from the recently maturing 0+ cohort (i.e. the prominent cohort in terms of abundance) that are close to 12 months of age, with only small numbers of the 1+ cohort (now nearly 24 months old) found during this time, particularly for females. This indicates that a large percentage of the female population will spawn during one season only, towards the end of their first year of life. However, it is possible that females spawn more than once during a season. The much greater investment in reproduction by female than male *M. dalli* during the time of faster growth is likely to increase their physiological stress and may explain the significant decline in the catch of females after the main period of reproduction (i.e. after March, Fig. 6).

4.2. Growth

Like the pattern of reproduction, *M. dalli* also exhibited a strong seasonal growth pattern. Most growth occurred during the warmer months from October to March. In their first five to six months of life, female and male *M. dalli*, on average, grow to approximately 10 to 12 mm carapace length (CL), respectively, and an estimated 0.88 to 1.47 g, respectively, in weight.

Growth remained very slow over the colder austral late autumn and winter months (May to August) until the following October when female *M. dalli* grew at a similar rate in length to that during their first six months (≈ 2 mm CL month^{-1}) but much faster in terms of weight (≈ 1 g month^{-1}). Following winter, the growth rate of males also increased but more slowly than that for females, reaching ~19 mm CL by March. Several fish species found in the Swan-Canning Estuary also exhibit the same pattern of highly seasonal growth (Wise et al., 1994; Veale et al., 2015). Water temperature has been shown to increase moulting frequency and thus increase growth rates in penaeids (e.g., Dall et al., 1990) and temperature is a key factor effecting their emergence from the sediments (Hill, 1985; Haywood and Staples, 1993; Wassenberg and Hill, 1994; Park and Loneragan, 1999) and hence vulnerability to fishing.

The von Bertalanffy instantaneous growth parameter, *K*, calculated from the Somers (1988) seasonal model were similar for females and males (both 0.98). However, the asymptotic carapace length (L_∞) was much larger for females (33.6 mm CL, ≈ 23.6 g wet weight) than males (22.8 mm CL, ≈ 9.3 g wet weight). It should be noted, however, that because of the high mortality rates for *M. dalli*, particularly females, few individuals are likely to reach the asymptotic size. The estimated L_∞ may therefore be an artefact of the model estimation process, with little biological meaning and the 95th percentile for length may be a better estimate of the asymptotic size for this species (see Hordyk et al., 2015).

The difference in growth patterns between females and males has been recorded in many species of penaeids (e.g. Primavera et al., 1998; Correa and Thiel, 2003; Callaghan et al., 2010; Mehanna et al., 2012; Accioly et al., 2013). The gender dimorphism recorded in the current study and that by Potter et al. (1986) (see also Fig. 9), where female *M. dalli* also grew much larger than males, is more than likely a life history strategy to maximise fecundity and optimise reproductive capacity of the population (Ramirez Llodra, 2002). Dall (1958), recorded similar differences in maximum size of female (30.5 mm CL) and male (24.1 mm CL) Greentail Prawns *Metapenaeus mastersii* (now *Metapenaeus ensis*) in the Brisbane river, although the size difference between genders was smaller than that recorded in the current study.

The estimates for the asymptotic length from the current study were 14 to 20% larger than those from over 30 years previously (28.0 mm CL and ≈ 14.44 g for females and 20.0 mm CL and 6.34 g for males) (Fig. 9, Table 2, estimated from figures in Potter et al., 1986) when the recreational fishery for school prawns was thriving. These differences in growth could be related to a range of biotic and abiotic factors, including increases in temperature and reductions in rainfall and consequently more persistent high salinities, as well as differences in fishing pressure and the sampling regimes in the thirty years between the studies. Prawns were sampled with greater frequency and at more sites in the current study than 30 years previously, particularly in the offshore waters with otter trawls. Although the mesh size of the otter trawls was similar during both studies, the hand trawl in the current study used smaller mesh (12 mm) than the historical study (19 mm). The difference in mesh size between the hand trawl nets should not adversely affect the catch of larger prawns (i.e., > 10 mm CL) and may not have affected that of small prawns due to the presence of material, such as macroalgae and jellyfish, which clog the mesh and gives the larger mesh net of Potter et al. (1986) a smaller effective net mesh size. An alternative explanation for the difference in L_∞, alluded to by Potter et al. (1986), is an increase in recreational fishing during the 1970s and 1980s, leading to increased fishing pressure and potential selection of larger prawns by fishers. Thus, over ≈ 78 nights of sampling in the shallows in the current study, only five groups of recreational prawn fishers were seen, whereas this was a common place activity thirty years ago involving up to 50,000 people each summer (Potter et al., 1986).

4.3. Mortality

The total instantaneous mortality rate (Z, assuming fishing mortality F ~ 0) estimated using the non-seasonal length-converted catch curve (LCC) method was nearly 60% higher for females (3.57 year^{-1}) than males (2.28 year^{-1}). This higher estimated mortality for females is consistent with the virtual disappearance of larger female *M. dalli* in the 1+ cohort after April, when the spawning season has completed (Fig. 6). Combined with a greater abundance of female than male prawns in the 0+ cohort, this provides strong evidence to suggest a higher rate of mortality in the female than male *M. dalli*. Because of very low current level of fishing for *M. dalli* (i.e. $F \rightarrow 0$), these estimates of total mortality provide an estimate close to those for natural mortality (*M*). The weekly instantaneous rates of mortality (females = 0.069; males = 0.043) are similar to the estimated *M* values for the juvenile stages of other species of penaeids, such as *Penaeus esculentus*, *P. semisulcatus* (Loneragan et al., 1994; Ye et al., 2005; Loneragan et al., 2006) and *P. merguiensis* (Haywood and Staples, 1993). The estimates of mortality for *M. dalli* have not taken into account changes in mortality with size, which Lorenzen (2000) has demonstrated can be very significant.

4.4. Implications for restocking

The highly seasonal pattern of growth implies that releases during the austral late autumn/winter should be avoided as growth during this time is very slow. The densities of *M. dalli* recorded in the current study, estimates of area covered by each net and assumed *M. dalli* catchability of 0.4 for both hand trawl and otter trawl nets (see Methods 2.3, Joll and Penn, 1990; Loneragan et al., 1995), gives an estimated biomass in the Swan-Canning Estuary of about 2.4 tonnes (Broadley et al., Murdoch University, unpublished data). This estimated biomass for *M. dalli* is only 16% of the maximum commercial catch for prawns (both *M. dalli* and the Western King Prawn *Penaeus* [= *Melicertus*] *latisculatus*) recorded from the system during the peak of the commercial fishery in the 1950s (Smith, 2006). The current biomass of *M. dalli* thus appears to be very low and has not recovered since recreational fishing decreased greatly in the late 1990s, over 15 years ago. Possible explanations of the suppressed *M. dalli* are an allee effect at low population densities (i.e. the rate of reproduction decreases at low population densities) and/or a change in environmental conditions in the Swan-Canning Estuary. Since *M. dalli* are not found in the local coastal waters, the population has little chance of recruitment from sources outside the Swan-Canning Estuary (Potter et al., 1986).

4.5. Conclusions

This study has established that the *M. dalli* population in the Swan-Canning estuary exhibits strong seasonal growth and reproductive cycles, similar to those described by Potter et al. (1986) over 30 years ago, when this species was more abundant and supported an iconic recreational fishery. Most of the growth occurs during the warmer months between October and March, with little to no growth in the colder months from May to August. Thus, cultured individuals should be released during the warmer months when prawns grow most rapidly. Reproductively active females were only found between October and March, with most reproduction concentrated in the months from November to February when surface and bottom water temperatures were between 20 and 28 ºC. The high mortality of the population and absence of larger, older *M. dalli*, particularly females, is a concern, as it appears that the majority of females are only spawning for one season, although possibly releasing eggs more than once during this season. Given the low estimated biomass of *M. dalli* in the Swan-Canning Estuary and lack of connectivity with populations in other estuaries to the north and south of this system, restocking has potential to increase the spawning population, provided environmental conditions are suitable.

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Table 1. The von Bertalanffy growth parameters for female and male *Metapenaeus dalli* estimated using the non-linear least squares (NLS) function from the Minpack package (Gayanilo et al., 2005a) for the current study and those estimated from the data in Potter et al. (1986). CI = 95% confidence Interval. $L(t)$ = average length at time t; L_∞ = asymptotic length; K = rate at which length reaches the asymptotic length; t_0 = theoretical time where the average length = 0; t_s = start of the curved portion of the first growth oscillation; C = controls the amplitude of the growth oscillation during the winter period (C = 1 - growth stopped, if C = 0 – continuous growth, i.e. no seasonal oscillation).

Years/Sex	L_∞ **(CI)**	K **(CI)**	t_0 **(CI)**	t_s	C
2013-2015					
Female	33.6 (30.9 - 34.4)	0.98 (0.98 - 1.17)	0.15 (-0.01 – 0.21)	0.12	1.00
Male	22.8 (21.6 - 24.4)	0.98 (0.84 - 1.12)	0.00 (-0.06 – 0.06)	0.09	0.90
1977-1982					
Female	28.0 (26.4 - 29.8)	1.05 (0.87 - 1.26)	-0.16 (-0.20 - 0.12)	-0.14	0.89
Male	20.0 (18.8 - 21.7)	1.01 (0.80 - 1.20)	-0.26 (-0.50 - 0.19)	-0.06	1.00

Table 2. Annual and weekly instantaneous mortality rates (*Z*) and 95% confidence intervals (CI) for female and male *Metapenaeus dalli* estimated from data collected in hand trawls and otter trawls from October 2013 to September 2015 using the non-seasonal Length Converted Catch Curve (LCC) method.

Sex	**Instantaneous total mortality *Z* (CI)**	
	***Z* year^{-1} (CI)**	***Z* week^{-1} (CI)**
Female	3.57 (3.28 - 3.86)	0.069 (0.063 - 0.074)
Male	2.28 (1.91 - 2.65)	0.043 (0.037 - 0.051)

Figure captions

Figure 1. Map showing (a) Australia and the distribution of *Metapenaeus dalli* in inshore marine waters (light grey) and solely in estuaries (dark grey) and (b) location of the 20 nearshore sites and 16 offshore sites in Swan-Canning Estuary sampled over 26 lunar cycles in the two years between October 2013 and October 2015. Dotted lines denote the separation among the five regions of the estuary.

Figure 2. Monthly total rainfall (mm, histogram) and average maximum temperature (line) for Perth between October 2013 and October 2015. Data obtained from the Bureau of Meteorology (http://www.bom.gov.au/climate/data/).

Figure 3. Monthly values for (a) surface and (b) bottom water temperature and (c) surface and (d) bottom salinity recorded in each of the five regions of the Swan-Canning Estuary between October 2013 and October 2015. Data sourced from the Department of Water (http://wir.water.wa.gov.au).

Figure 4. The number of female and male *Metapenaeus dalli* caught in each 1 mm carapace length class size from (a) hand and (b) otter trawls samples collected over 26 lunar cycles between October 2013 and October 2015. N = 1,323 for hand trawls, N = 9,247 in otter trawls.

Figure 5. The logistic regression fitted to the proportion of gravid females in each 1 mm CL during the breeding season, i.e. October to March, (solid line) to estimate the size at maturity for female *Metapenaeus dalli* in the Swan-Canning estuary. The dashed line represents the carapace length where 50% (CL_{50}) of females are mature.

Figure 6. Monthly carapace length (mm) frequency histograms for female *Metapenaeus dalli* in 1 mm length classes from hand and otter trawl samples obtained every 28 days (lunar cycle) between October 2013 and September 2015 in the Swan-Canning estuary. Normal distributions (dashed lines) were fitted to identify the mean, SD, weighting and number of prawns in each cohort (labelled A to F). Note no data are shown for December 2014, when an engine failure prevented sampling with the otter trawl.

Figure 7. Monthly carapace length (mm) frequency histograms for male *Metapenaeus dalli* in 1 mm length classes from hand and otter trawl samples obtained every 28 days (lunar cycle) between October 2013 and October 2015 in the Swan-Canning estuary. Normal distributions (dashed lines) were fitted to identify the mean, SD, weighting and number of prawns in each cohort (labelled A to F). Note, no data are shown for December 2014, when an engine failure prevented sampling with the otter trawl.

Figure 8. The mean carapace length (± 1 SD) for the cohorts identified in the analysis of the carapace length frequency distributions in Figure 6 for female and Figure 7 for male *Metapenaeus dalli* in each lunar cycle between October 2013 and September 2015 in the Swan-Canning estuary.

Figure 9. Growth models fitted to estimated using Somers' (1988) seasonal adaption of the von Bertalanffy growth model fitted to mean carapace lengths for (a) female and (b) male *Metapenaeus dalli* collected in 2013/15 and (c) female and (d) male *M. dalli* collected in 1977-82. Points for the 2013/15 data show the mean observed values from the length frequency distribution for cohort F for females (Figs 6, 8) and D for males (Figs 7 and 8). Solid line is the line of best fit, with dashed lines showing 95% confidence intervals.

Figure 10. Non-seasonal length converted catch curves for (a) female and (b) male prawns showing the relationship between the rate of change in numbers (ln[N/dt]) with the relative age for *Metapenaeus dalli* caught between October 2013 and September 2015 in the Swan-Canning estuary. Dotted curve shows the catch-curve used to estimate total mortality (see Methods 2.6, Table 2).

Figure

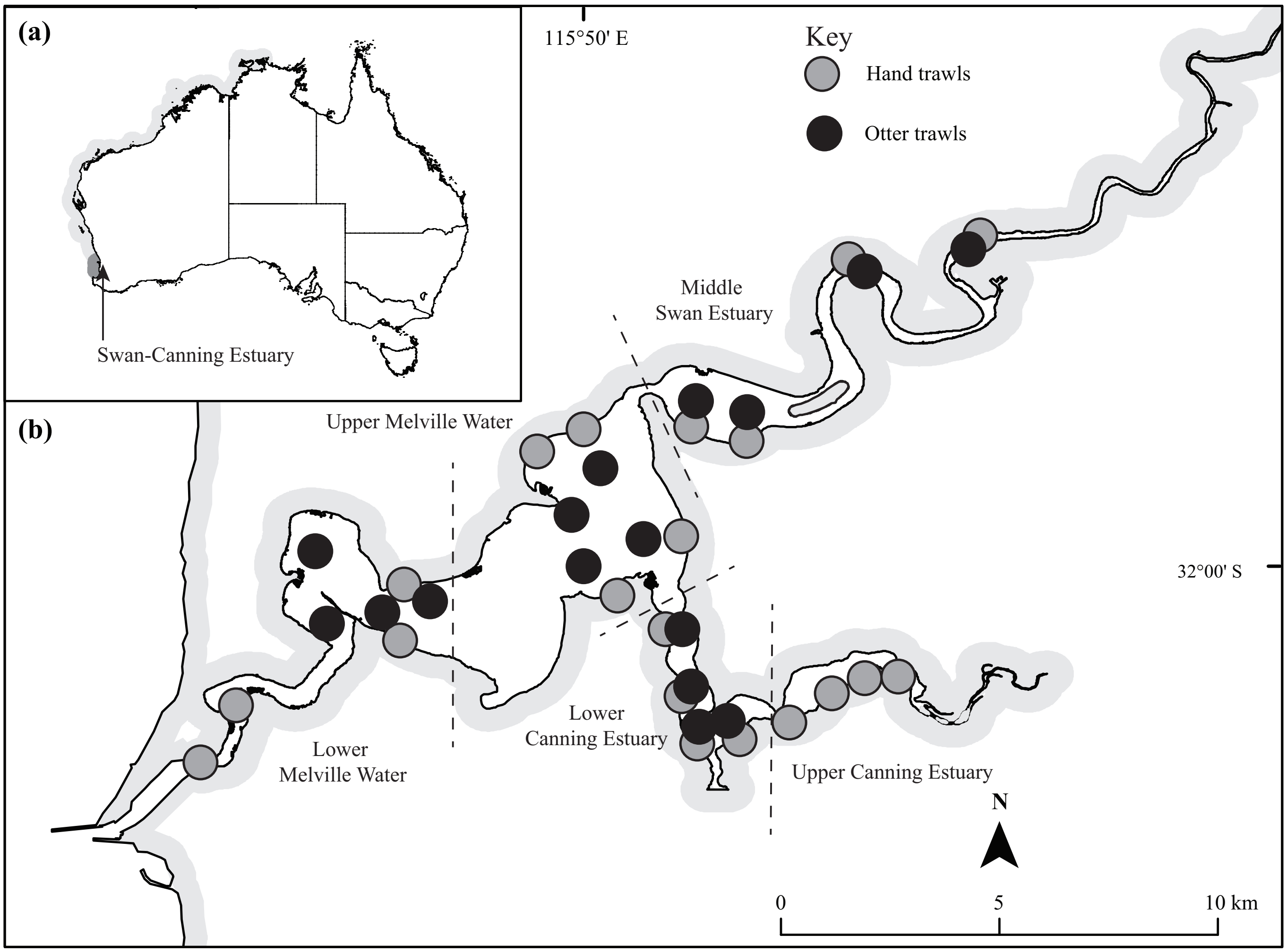

Figure 1.

Figure

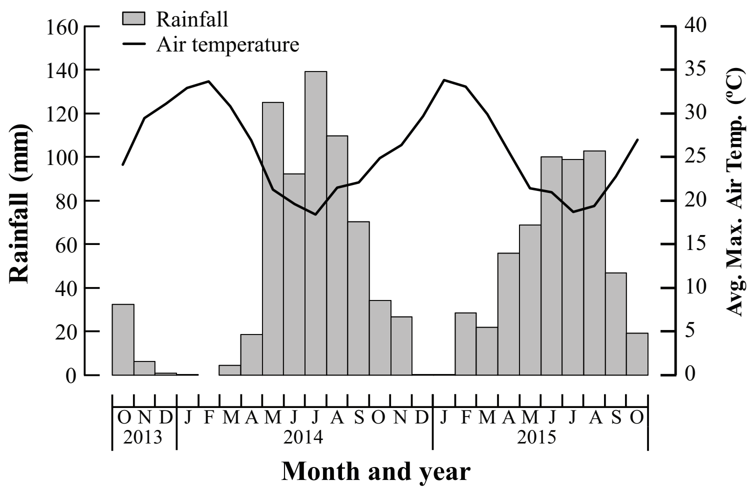

Figure 2.

Figure

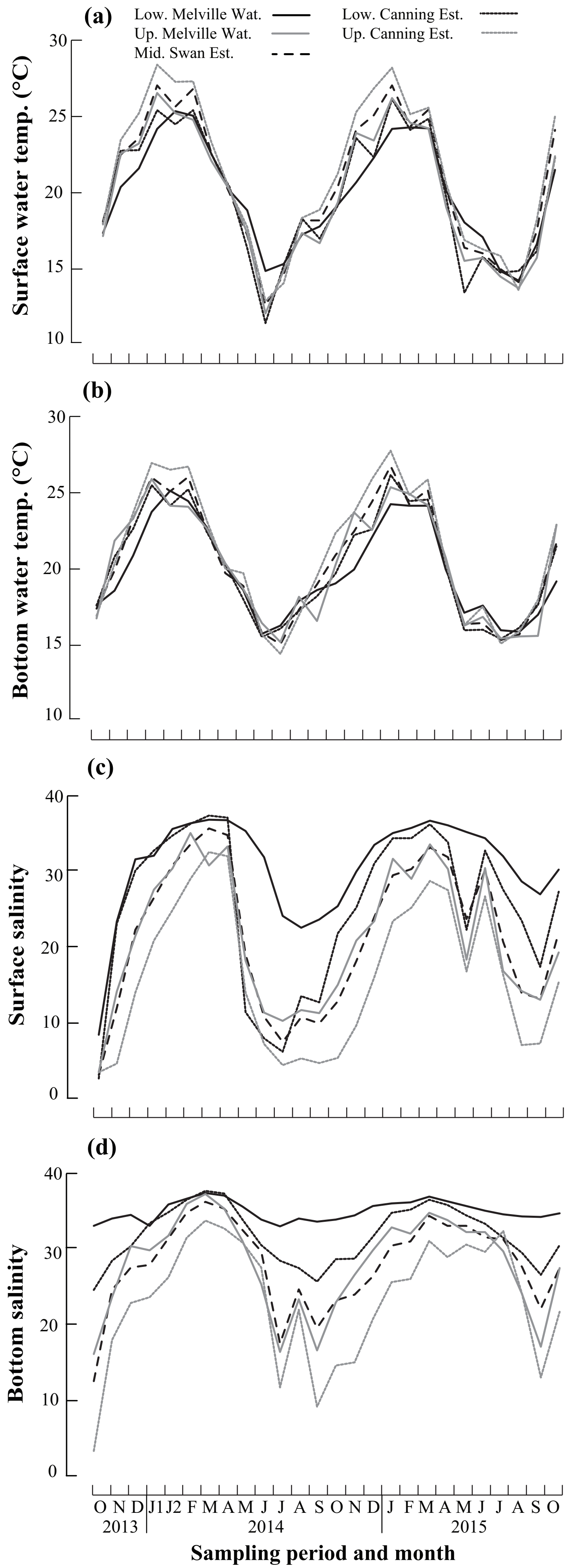

Figure 3.

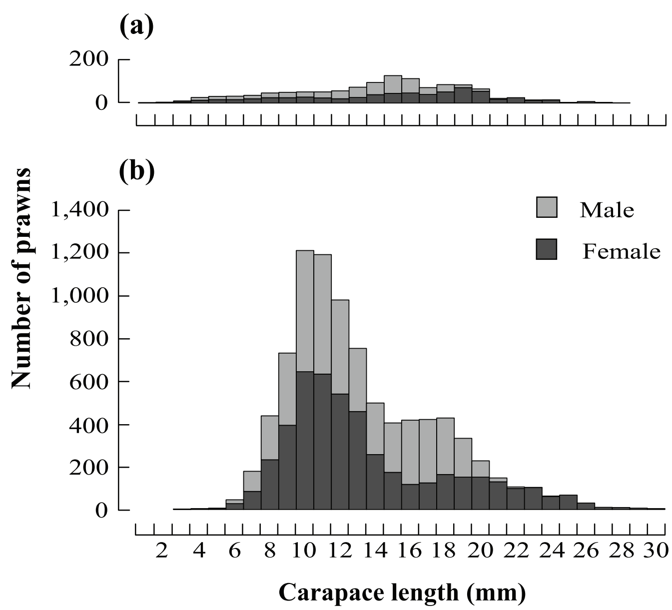
(a)
200
0
(b)
Number of prawns
1,400
1,200
1,000
800
600
400
200
0
Male
Female
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Carapace length (mm)

Figure 4.

Figure

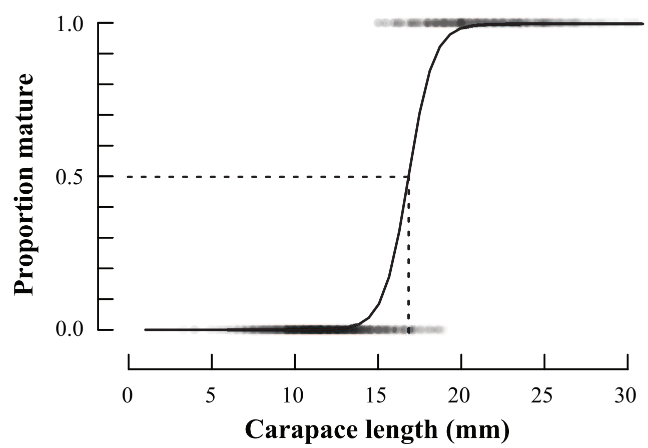

Figure 5.

Figure

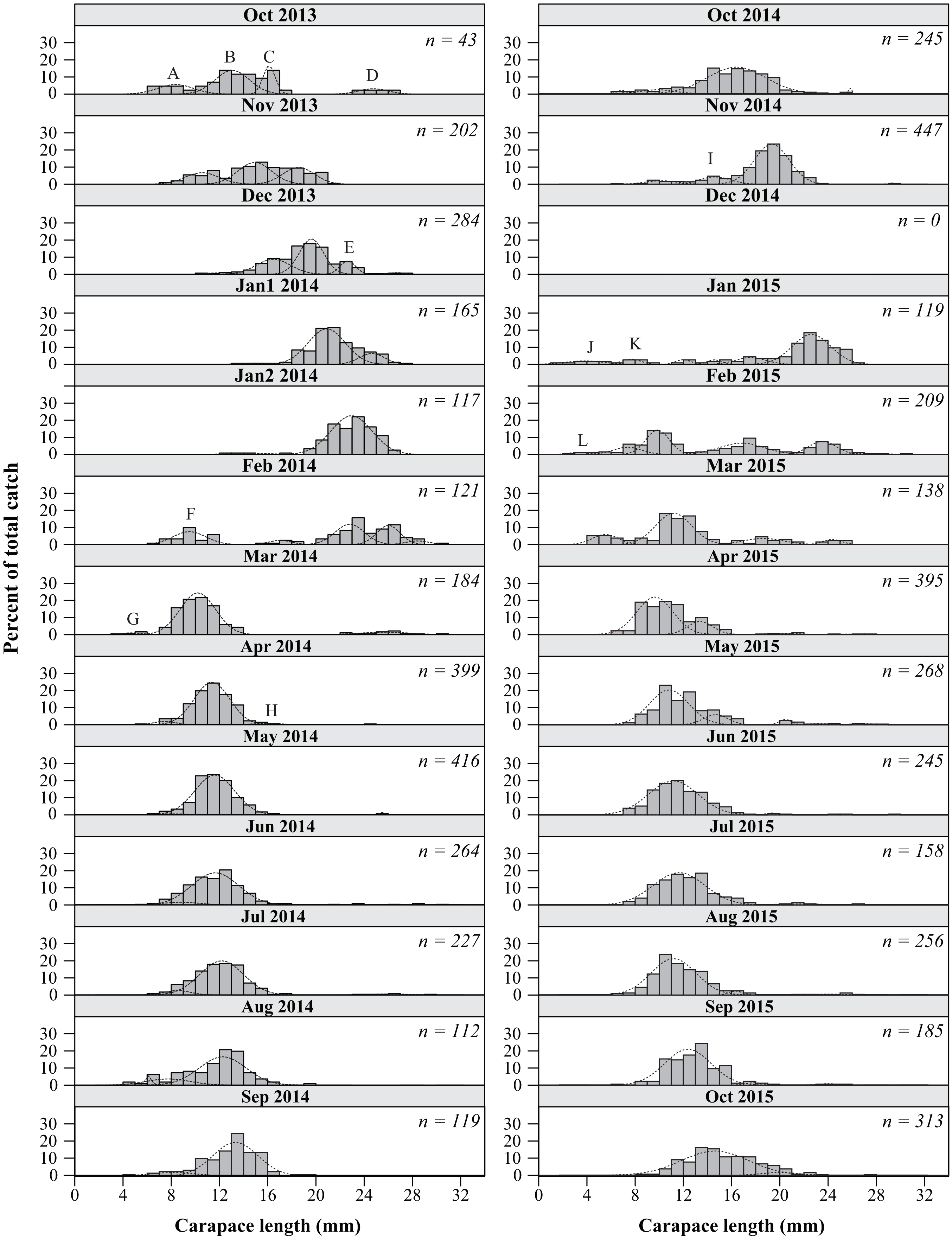

Figure 6.

Figure

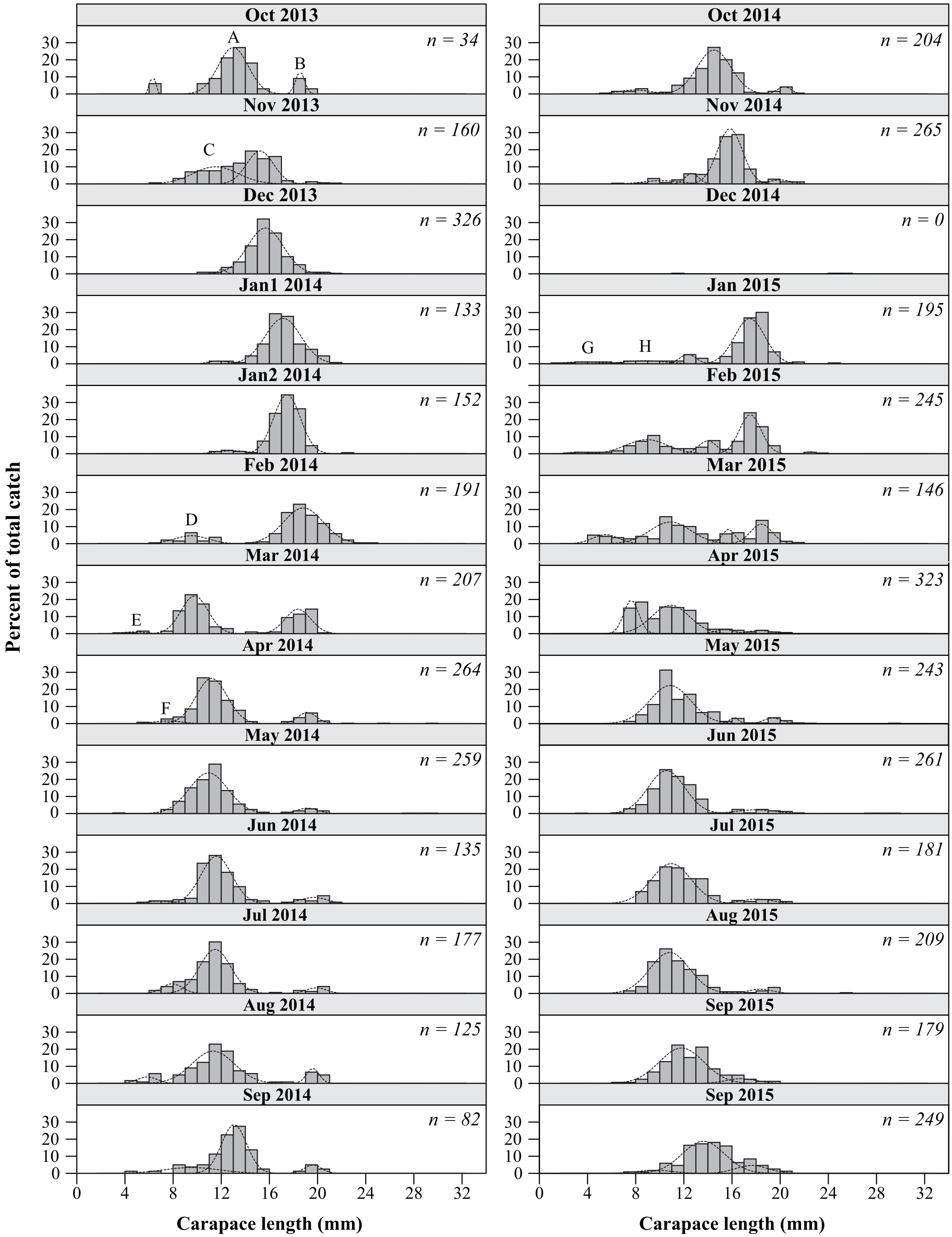

Figure 7.

Figure

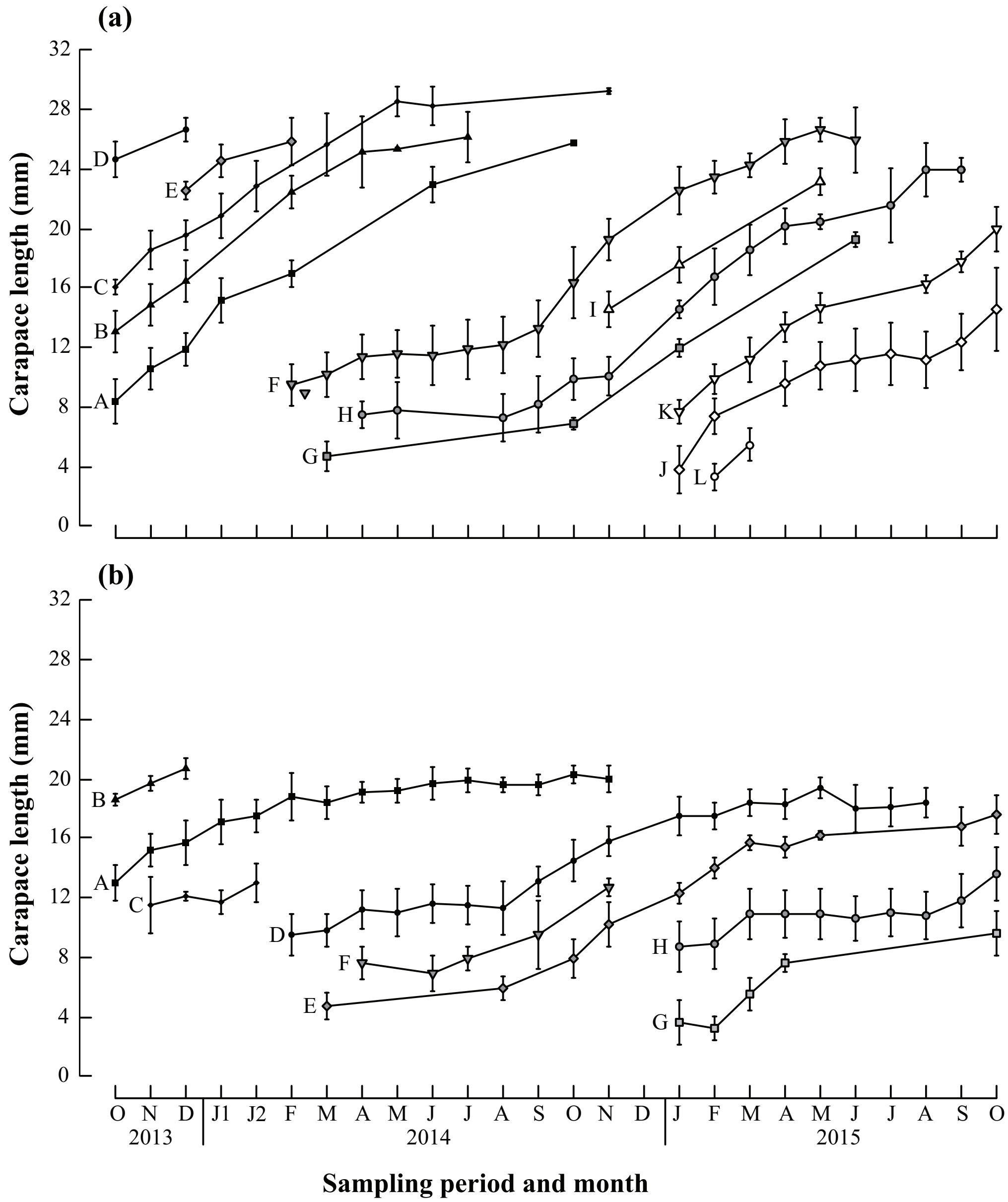

Figure 8.

Figure

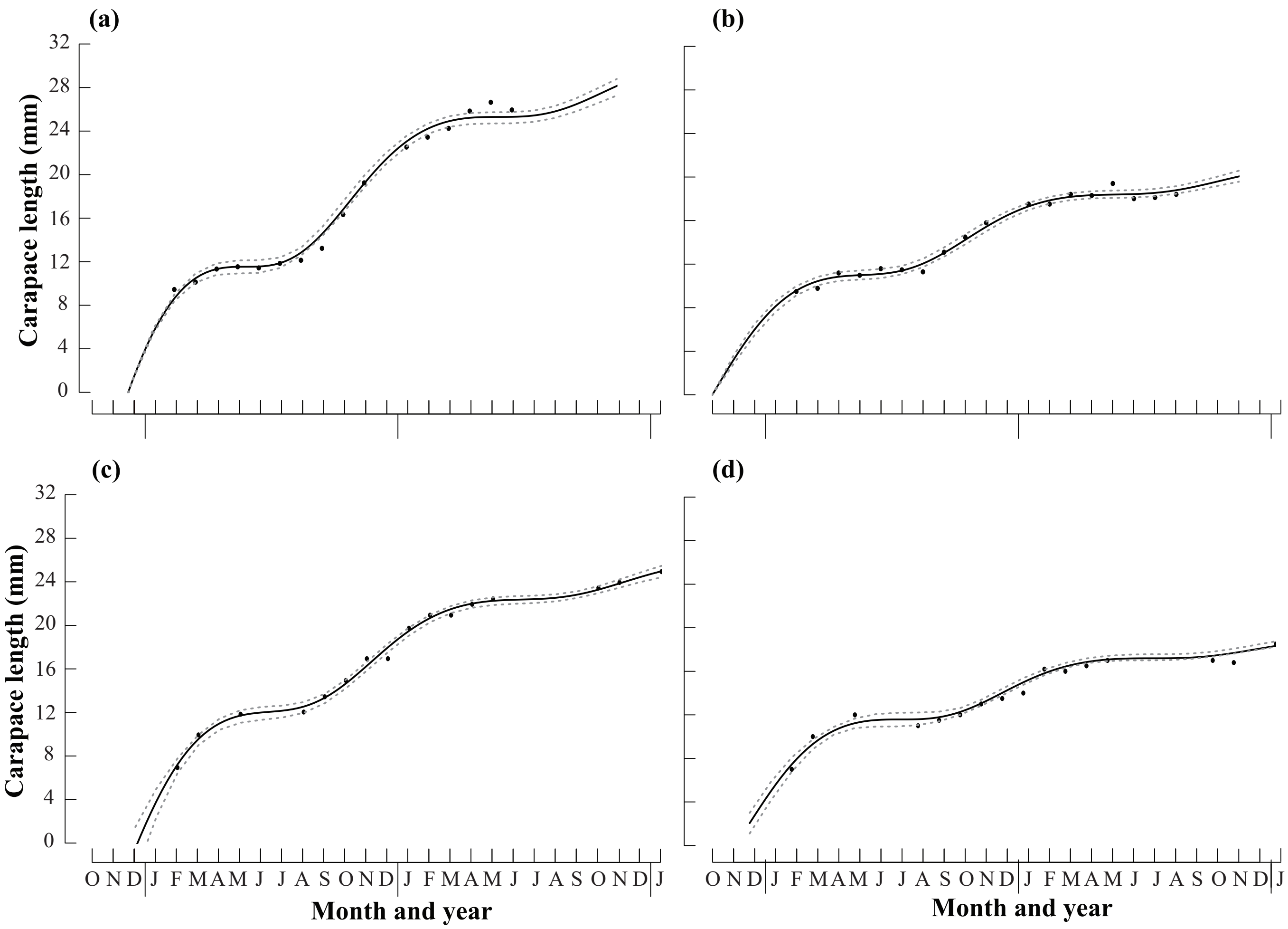

Figure 9.

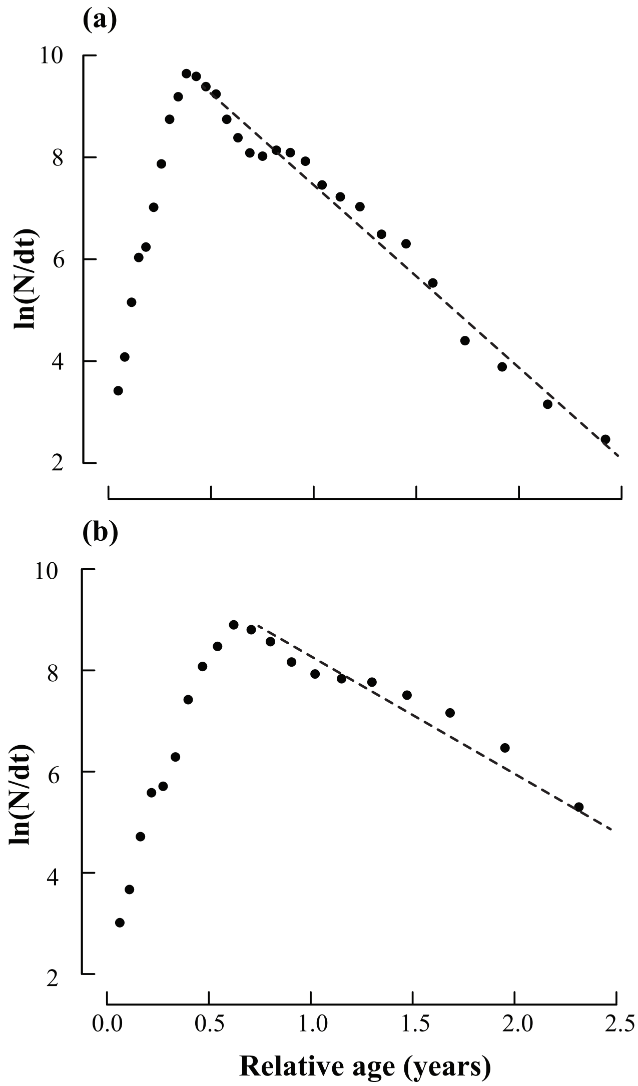
(a)
10
8
6
4
2
ln(N/dt)
(b)
10
8
6
4
2
ln(N/dt)
0.0
0.5
1.0
1.5
2.0
2.5
Relative age (years)

Figure 10.